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1 **Chimpanzees (*Pan troglodytes*) develop a successful communicative strategy to collaborate**

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23 **Abstract**

24  
25 Successful collaboration often relies on individuals' capacity to communicate with each other.  
26 Despite extensive research on chimpanzee communication, there is little evidence that chimpanzees  
27 are capable, without extensive human training, of regulating collaborative activities via  
28 communication. This study investigated whether pairs of chimpanzees were capable of  
29 communicating to ensure coordination during collaborative problem-solving. The chimpanzee pairs  
30 needed two tools to extract fruits from an apparatus. The communicator in each pair could see the  
31 location of the tools (hidden in one of two boxes), whereas only the recipient could open the boxes.  
32 The subjects were first successfully tested for their capacity to understand the pointing gestures of a  
33 human who indicated the location of the tools. In a subsequent conspecifics test, the communicator  
34 increasingly communicated the tools' location, by approaching the baited box and giving the key  
35 needed to open it to the recipients. The recipient used these signals and obtained the tools, transferring  
36 one of the tools to the communicator so that the pair could collaborate in obtaining the fruits. The  
37 study suggests that chimpanzees have the necessary socio-cognitive skills to naturally develop a  
38 simple communicative strategy to ensure coordination in a collaborative task.

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42 **Keywords:** collaboration, chimpanzees, coordination, communication

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Human communication often involves individuals informing recipients of things that they believe will be useful or relevant to them (1). It has been hypothesized that such skills and motivations may have evolved in the context of mutualistic collaboration, in which one partner helping another by providing relevant information ends up benefiting both of them (2-4).

Despite extensive research on chimpanzee communication (5-7), we know very little about their naturally occurring communicative strategies to support collaborative activities, such as group hunting and boundary patrols. Of particular interest are instances of communication intended to facilitate coordination and success when individuals pursue a common goal. There is evidence of communication to coordinate travel to desired locations. In a classic study by Menzel (8-9), chimpanzees followed a knowledgeable leader to a location where food had been hidden. Leaders occasionally encouraged their partners to follow them and naïve individuals learned to read the leader's behavior. There is also evidence of a vocalization to coordinate travel, the "travel hoo", given prior to departure to recruit other group partners, especially allies (10). In these previous studies, attempts to communicate were made mainly to encourage partners to follow (for selfish or prosocial reasons), but not to inform them about anything in particular, nor to influence a collaborative activity coordinating different roles, since leaders can ultimately also start moving alone.

We refer to *collaborative* activities as mutually beneficial activities in which two or more individuals coordinate their actions to obtain a common resource or produce an effect that one individual would not be able to produce on her or his own. Chimpanzees are capable of intentionally coordinating their actions with a partner in collaborative tasks (11-13). They wait for their partner before initiating the collaborative activity and they even recruit the most skillful partner (11,12). They also help their partners instrumentally, by giving them the tools they need to perform their role (13). The focus of this study was on investigating whether chimpanzees are able to coordinate through communication in a mutualistic collaborative task.

A few instances of communication during collaboration have been observed in experiments in which one chimpanzee tried to encourage a human partner to act in some way in order to obtain an out-of-reach reward. In these studies chimpanzees approached the human, seized him by the arm and brought him closer to the problem they were trying to solve in an effort to get the human to obtain the reward for them or get help from them (14-15) (see also 16, but see 17 for negative findings). Evidence for communication between collaborating chimpanzees is scarcer. In a study by Crawford (18), pairs of chimpanzees were trained to pull together to bring a heavy baited box within reach. Occasionally, a chimpanzee lost motivation and stopped pulling and the partner employed various soliciting gestures to encourage the partner to continue pulling. Bullinger et al. (19, see also 20) also found some instances of intentional communication in a stag-hunt game scenario. In this coordination game individuals can choose between hunting alone the lower-quality "hare" or cooperating with the partner to obtain the higher quality "stag. In this study, chimpanzees used 'attention-getters' to get the partner to follow them, once they were already at the stag (19).

In all these previous studies, attempts to communicate were made to reactivate partners, encouraging them to 'do something' or 'follow me', but not to inform them about anything in particular, nor to coordinate roles. Only two previous paradigms, one with language-trained chimpanzees (21-22) and one of our own (23), have investigated whether chimpanzees support collaboration partners by providing the information they need to perform their role.

Savage-Rumbaugh et al. (21) trained two chimpanzees to use a lexigram keyboard that simulated human linguistic symbols. In the collaborative task one individual had to identify a specific tool to open a reward box and use the lexigram to request the tool, whereas the partner had to retrieve the specified tool and give it to the requester, who was then able to obtain the food. The two individuals underwent several training phases that required between 500 and 600 trials. First, they were introduced to the functionality of the different tools and had to learn to request the tools in order to obtain food for themselves. Afterwards, they were trained to name the tools: either they had to name the tool displayed by the human experimenter (E), or select the tool requested by E. Once they had mastered both roles of the task (encoding and decoding) with the human partner, the two chimpanzees were paired together. Initially the chimpanzees requested the tool from the experimenter, and the partner just played with it or dropped it. However, the experimenter facilitated collaboration

101 between the two chimpanzees by communicating she had no tools and encouraging subjects to look  
102 and pay attention to each other (by pointing) so that after several trials, they started to realize they  
103 could request tools from each other.

104 This study showed that with artificial means, i.e. a trained symbolic system, and human  
105 training chimpanzees can learn to request tools from each other and comply with these requests in the  
106 context of a collaborative interaction. However, we do not know whether they can solve similar  
107 problems in the absence of training and an artificial communicative system. Furthermore, in the  
108 previous paradigm they were first trained to perform both roles (communicator and recipient) with a  
109 human partner, and nevertheless the experimenter had to intervene during the conspecifics test to  
110 facilitate collaboration and communication between them. Therefore, it is questionable to what extent  
111 they grasp the interdependency of their roles and could naturally, and without human training, solve a  
112 similar collaboration problem dependent on coordination and communication between partners.  
113

114 In a previous study(23), we attempted to investigate this question and created a context in  
115 which chimpanzees could help partners play their roles either by transferring the needed tool or by  
116 communicating the hiding place of the needed tool. Although the chimpanzees readily helped each  
117 other by transferring the tool (as in 13), they did not reliably communicate the location of the hidden  
118 tool, nor comprehend their partner's communicative behaviors. Communicators sometimes positioned  
119 themselves in front of the hiding location, and occasionally combined this behavior with overt  
120 communication (e.g. stomping, jumping, mesh-banging). However, the recipients did not follow these  
121 signals, so that communicators stopped communicating. If the recipients had paid attention and  
122 followed the occasional communicator's signals, the communicator's behavior might have been  
123 positively reinforced, leading to a spiraling of successful production and comprehension of  
124 communicative signals.

125 That recipients did not follow the communicator's signals is maybe not surprising given that  
126 there is mixed evidence about chimpanzees and other great apes' capacity to understand informative  
127 social cues. In some studies, some chimpanzees have been found to be capable of using pointing to  
128 make an informed choice about which container to select (24-27, see 28 for review). However, in  
129 other studies chimpanzees have failed to make use of such cues (e.g. 29-33). Enculturated apes  
130 typically perform better than non-enculturated apes (34- 36) (although see 37), although the level of  
131 enculturation of many of the successful subjects goes well beyond a rich socio-communicative  
132 environment, since many of these subjects were language trained apes that underwent extensive  
133 training designed to foster human-chimpanzee communication. Therefore, one may question to which  
134 extent their use of social cues is based on simple associative processes that only emerge after  
135 extensive training (29). Alternatively, apes' difficulty to use social cues could be due to attentional  
136 constraints, since the salience of the signals also seems to play a role and adding vocalizations to  
137 bodily gestures seems to facilitate subjects' understanding, even among non-enculturated apes  
138 (24,25,38). There is also some evidence that distal set-ups, in which subjects must choose between  
139 containers that are further apart (>100cm) or approach the container to choose from a distance, also  
140 improve subjects' comprehension of communicative signals, the reason potentially being that the  
141 proximal set-up prevents subjects from paying attention to the experimenter's signals (27,39). In  
142 summary, there is evidence for chimpanzees' pointing comprehension but also many studies in which  
143 they perform rather poorly, and the exact factors that contribute to pointing comprehension are not  
144 well understood.  
145

146 In the current study we tested whether pairs of chimpanzees would find a way of communicating the  
147 location of tools that the pair needed to obtain food. The chimpanzees had previously participated in  
148 the collaborative task (13, see Fig. 1a). However, we added a new level of complexity by hiding in  
149 one of two possible locations the tools they needed to collaborate. We were interested in both the  
150 production and the comprehension side of the interaction. The communicator in each pair could see  
151 the location of the tools, whereas only the recipient could open one of the boxes (see Fig. 1c,d). After  
152 obtaining the tools, the recipient needed to transfer one of the tools to the communicator so that each  
153 individual could perform her role in extracting the grapes.  
154

155 The subjects participated in three experiments. In experiment 1, we investigated chimpanzees' ability  
156 to understand the communicative signals of a human partner. All ten subjects played the recipient

157 role, and a human partner pointed distally to the location of the tools. In experiment 2, we focused on  
158 chimpanzees' tendency to communicate the location of the tools intentionally. The five pairs of  
159 chimpanzees (n = 10) played both roles (communicator and recipient). In the test condition, the  
160 communicators could communicate the location of the tools to the recipients, and in the control  
161 condition the recipients were absent to test the intentionality of the communicators' behavior. Since  
162 the chimpanzees increased their communication as experiment 2 progressed, we conducted  
163 experiment 3 to investigate recipients' comprehension as the communicators communicated more  
164 reliably. In experiment 3, subjects received additional trials of the test condition of experiment 2. A  
165 new group of chimpanzees (n = 6) participated in a follow-up control condition to test whether the  
166 recipients' behavior could be explained with a local enhancement mechanism.

## 167 **Methods**

### 169 **Subjects**

171 Ten chimpanzees (six females, four males) living at Sweetwaters Chimpanzee Sanctuary, Kenya  
172 participated in this study. All ten subjects had previously participated in (13) and were familiar with  
173 the collaborative task employed in this study. In addition, six other chimpanzees participated in the  
174 control condition of experiment 3 (SI Materials and Methods).

### 176 **Apparatus**

177 The collaboration apparatus consisted of a transparent box placed between two testing rooms (13).  
178 The individual facing the back of the box was required to insert a thin stick and rake the grapes,  
179 whereas the individual facing the front of the box was required to insert a long stick through a hole on  
180 the left side of the box and push to tilt the platform (Fig. 1a). Two identical opaque boxes, attached  
181 between two testing rooms, served as hiding locations for the tools (see Fig. 1b,c,d). Each box had a  
182 small transparent window on the back and a guillotine door on the front, which could only be opened  
183 by inserting a key below the door. The door only opened once the key was completely pushed inside  
184 to prevent subjects from pulling the key out to re-use it to open the second box.

### 187 **Procedure and Design**

#### 188 **Pre-tests**

189 The subjects were individually introduced to the different contingencies of the hiding boxes (pre-tests  
190 1 to 4, see SI Materials and Methods). In the last individual metacognition pretest (pretest 4), subjects  
191 had to look through the windows on the backs of the boxes to determine the location of the rewards  
192 before choosing which box to open (see Fig. 1b and Video 1). We were less interested in their  
193 metacognitive skills per se than in using this pre-test as a necessary prerequisite for participation in  
194 the communication test. If chimpanzees searched for the required information before opening one of  
195 the boxes, they might also be more likely to use the information provided by the communicator. There  
196 were considerable individual differences in how quickly subjects started to check the contents of the  
197 boxes before opening one of them (see supplementary materials for further details). This fits with the  
198 results of previous studies of primates' metacognitive capacities (40-41). Dyads also received a  
199 couple of reminder collaboration sessions, in which they had to transfer one of the tools to their  
200 partner in order to collaborate obtaining the grapes (pre-tests 5 and 6, see SI Materials and Methods).

202 Experiment 1: The set-up was as in the conspecifics test (Fig. 1c,d), except that the human (E1)  
203 positioned herself in Room 1, equidistant from the two hiding boxes. The tools were hidden in one of  
204 the hiding boxes and the key to open the hiding boxes was placed equidistantly between the two  
205 hiding boxes in Room 2. The moment the subject started to enter Room 2, E1 called the subject's  
206 name and food-grunted while being slightly bodily oriented, looking at and pointing (cross-pointing)  
207 to the baited box. Each subject participated in two sessions of six test trials each.

#### 209 **Experiment 2: Cooperative communication between chimpanzees – focus on production**

210 Each test session consisted of four different kinds of trial, beginning with two introduction trials,  
211 followed by two trios of trials. Each trio comprised one trial of each type (i.e. test, control and  
212 motivation) in a randomized order (SI Materials and Methods). In the test trials (Fig. 1c,d), the

213 collaboration box was baited with eight grapes. The two hiding boxes were closed, and one contained  
214 the tools. The communicator in Room 1 was able to see the content of the hiding boxes. If the  
215 recipients opened the correct box and obtained the tools, they had to transfer the raking tool to the  
216 communicator so that they could collaborate in obtaining the grapes. The control trials were as the test  
217 trials, except that the recipient never entered Room 2. The motivation trials were similar to the test  
218 trials, except that the two hiding boxes were open and one contained the tools (i.e. the recipients were  
219 able to obtain the tools straight away). In half of the test and control sessions, the key to the hiding  
220 boxes was placed in Room 2 (mid-way between the two hiding boxes), whereas in the other half of  
221 the sessions, the communicators had the key. All dyads participated in six sessions (two trials of each  
222 type per session), after which the subjects exchanged roles (i.e. communicators became recipients and  
223 vice versa) and participated in another six sessions.

224  
225 Experiment 3: Cooperative communication among chimpanzees – focus on comprehension  
226 Each test session started with four introduction trials, in which the communicator was absent, and the  
227 hiding boxes were empty, followed by six test trials like in Exp. 2, except that now the communicator  
228 always had the key. The subjects received a total of 18 test trials. The follow-up control experiment  
229 was conducted with a new group of six subjects. They also received sessions of four introduction  
230 trials, followed by six test trials (total of 18 test trials) in which there was no communicator and  
231 subjects encountered the key positioned close to the baited box (see SI Material and methods).

232  
233 Coding and Analysis  
234

235 All trials were videotaped and a second observer independently scored 30% of the trials for reliability  
236 purposes. We coded which of the hiding boxes subjects opened and all instances of behavior directed  
237 to indicate one of the boxes. We coded as communicative behaviour all instances of behaviour in  
238 which the communicators positioned themselves close to (or behind) one of the boxes, and touched,  
239 looked at the box or gave to the recipient the key close to it before the recipients started to open one  
240 of the boxes (see SI Materials and Methods for further details on coding methods and inter-observer  
241 reliability). We used non-parametric tests to compare subjects' performance with chance outcomes.  
242 Furthermore, given that we had individuals in each dyad playing both roles (communicator and  
243 recipient) and all dyads received multiple trials, we also analyzed the data using Generalized Linear  
244 Mixed Models (GLMM) (42), and included the identities of the dyad, the communicator and the  
245 recipient as random factors to control for the non-independence of the data. Since our responses were  
246 always binary, the models were fitted with binomial error structure and logit link using the function  
247 `glmer` of the R-package `lme4` (43-45). Each full model was compared to a null model that included the  
248 control predictors and random effects by using a likelihood ratio test (46). As random effects we  
249 included random intercepts for the dyad and the communicator (since normally each communicator  
250 only had one recipient). Furthermore, to keep type I error rates at the nominal level of 0.05 we  
251 included various random slopes (47-49). Please refer to the electronic supplementary material for  
252 more details on each of the models. The datasets supporting this article have been uploaded as part of  
253 the supplementary material.

254  
255 **Results**

256 In experiment 1 the human partner indicated the location of the tools by calling the subject's  
257 name and food-grunting to get the chimpanzees' attention and using cross-pointing and gaze  
258 alternation between the subject and the baited box (see Video 2). As a group the chimpanzees  
259 performed above chance and followed the human pointing in 81% of trials ( $P = 0.02$ , exact Wilcoxon  
260 signed-ranked test,  $n = 10$ ,  $T+ = 55$ ). Five out of the ten subjects performed individually above  
261 chance. After obtaining the tools, the chimpanzees transferred the raking tool to the human  
262 experimenter, who then collaborated with the subject to obtain the grapes.

263 In Experiment 2, pairs of chimpanzees were required to communicate with each other. We did not  
264 observe any gestures (i.e. pointing) or attempts to signal the boxes from a distance, but we observed a  
265 clear and effective strategy to signal one of the boxes and influence the partner's choices. Subjects'

266 communicative behavior consisted of approaching and positioning themselves behind or very close to  
267 one of the boxes just before recipients could make a choice, sometimes touching, looking at the box  
268 or giving the key to the recipient close to the box (see also the supplementary material and Videos 3  
269 and 4). We observed this behavior in 50% of trials of the test condition, and in only 20% of control  
270 trials when recipients were absent ( $P = 0.006$ , exact Wilcoxon signed-ranked test,  $n = 10$ ,  $T_{+} = 53$ , see  
271 Figure 3a). We also fitted a GLMM to test the effect of condition and trial on individuals' likelihood  
272 of communicating. We included communication as the dependent variable and as fixed factors the  
273 interaction between trial number and condition and the fixed factors: communicators' possession of  
274 key, role order and baited box (left/right). The full model was significantly different from a more  
275 parsimonious model without the interaction between trial number and condition, but all the fixed  
276 factors and the random intercepts and slopes (Likelihood ratio test:  $\chi^2(1) = 15.419$ ,  $p < .001$ ). The  
277 subjects were more likely to communicate in the test condition but less likely in the control condition  
278 with increasing trial numbers (estimate = 1.262, SE = 0.330,  $Z = 3.819$ ,  $P < 0.001$ ; Figure 3b),  
279 whereas the other factors had no effect (see SI for full model outputs). Throughout this experiment,  
280 the subjects seemed to learn the necessity of signalling the location of the tools when the recipients  
281 were present.

282 In experiment 2, the recipients opened the indicated box in 52% of trials with communication,  
283 which is not significantly different from a chance outcome ( $P = 0.54$ , exact Wilcoxon signed-ranked  
284 test,  $n = 10$ ,  $T_{+} = 23$ ). However, comparison between success levels in the absence or presence of  
285 communication shows that the subjects tended to be more successful when their partners  
286 communicated than when they did not ( $M = 52.79\%$  vs.  $M = 28.45\%$ ; exact Wilcoxon signed-ranked  
287 test:  $n = 10$ ,  $T_{+} = 38$ ,  $P = 0.07$ , see graph in SI for individual data). We fitted a GLMM to test the  
288 effect of "communication" on the recipients' likelihood of opening the box with tools. The full model  
289 included "Success finding the tools (yes/no)" as the dependent variable, and communication (yes/no),  
290 trial number, role order, communicator's possession of the key and baited box as fixed factors. The  
291 full model was significantly different from a more parsimonious model that included all control  
292 predictors (trial, role order, communicator's possession of the key and baited box) and the random  
293 intercepts and slopes (Likelihood ratio test:  $\chi^2(2) = 5.327$ ,  $p = .021$ ). The recipients were more likely  
294 to find the tools when their partners communicated whereas none of the other factors had any effect  
295 (estimate = 1.295, SE = 0.476,  $Z = 2.724$ ,  $P = 0.021$ ; see SI for full model output and additional  
296 model details). Given that communicators only communicated reliably as the experiment progressed,  
297 overall the dyads were not that successful.

298  
299 In experiment 3, the communicators signalled one of the boxes, by positioning themselves  
300 and transferring the key almost into contact with the baited box, in 81.11% of trials (range = 28  
301 100%) and they indicated the correct box (the one containing the tools) in 86% of trials with  
302 communication (range = 63–100%, see Fig. 4a), significantly more often than expected by chance  
303 (Wilcoxon exact test:  $N = 10$ ,  $T_{+} = 55$ ,  $p = 0.002$ ). We ran a GLMM to test whether individuals'  
304 likelihood of communicating the location of the tools increased with trial number (see SI Material and  
305 Methods). We included "correct communication" (yes/no) as the dependent variable (no  
306 communication or signalling the empty box were considered incorrect responses) and as fixed factors  
307 trial number, role order, and baited box. The full model was not significantly different from a more  
308 parsimonious model that included only role order and baited box as control predictors and the random  
309 intercepts and slopes. There was no evidence that subjects improved their communication with  
310 increasing numbers of trials (likelihood ratio test:  $\chi^2(1) = 0.066$ ,  $p = 0.798$ ). The subjects seem to  
311 have learned the need for communication in the previous experiment and started this new set of trials  
312 performing at high levels. Only two subjects (Amahirwe and Jojo) communicated very little, and their  
313 performance did not change throughout the experiment.  
314 In experiment 3, the recipients opened the box indicated by the partner in 81.11% of trials with  
315 communication which is significantly above chance levels ( $P = 0.002$ , exact Wilcoxon signed-ranked  
316 test,  $n=10$ ,  $T_{+} = 55$ ; see Fig. 4b). Overall, pairs succeeded in obtaining the tools in 69.8% of trials,  
317 which is also significantly above chance ( $P = 0.002$ , exact Wilcoxon signed-ranked test,  $n = 10$ ,  $T_{+} =$   
318 55). We fitted a GLMM to test the effect of "correct communication" on the recipients' likelihood of  
319 opening the box with tools. Since the subjects communicated at such high levels, we did not look at

320 simple communication but at ‘correct communication’ (i.e signalling the box containing the tools). We  
321 included “Success finding the tools (yes/no)” as the dependent variable, and correct communication,  
322 trial number, role order and baited box as fixed factors. The full model was significantly different from  
323 a more parsimonious model that included trial number, role order and baited box as control predictors  
324 and the random intercepts and slopes (Likelihood ratio test:  $\chi^2(1) = 6.267$ ,  $p = 0.012$ ; see SI for full  
325 model outputs).

326 The recipients were more likely to obtain the tools when their partners communicated  
327 correctly (estimate = 1.884, SE = 0.590, Z = 3.194, P = 0.012), whereas all other factors, including  
328 trial number had no effect on levels of success, suggesting that recipients chose to open the box  
329 indicated by the communicators from the outset of this new set of trials.

330 A low-level interpretation of the recipients’ behaviour could be that the subjects opened the  
331 box to which they were closest to when they got the key, without any understanding of their partners’  
332 communicative intentions. To rule out this explanation, we ran a control experiment with a new group  
333 of subjects. The human experimenter hid the fruit rewards in one of the boxes and cued the box by  
334 positioning the key close to it. The subjects opened the ‘cued’ box in 66.67% of trials, which is not  
335 above chance levels (P= 0.12, exact Wilcoxon signed-ranked test, n = 6, T+ = 14). We also conducted  
336 another analysis using these results (67%) as a baseline to which to compare recipients’ tendency to  
337 open the box indicated by their partners (81.11%), finding that the communicators’ behavior added  
338 something to simply finding a key next to one of the boxes (P = 0.02, exact Wilcoxon signed-ranked  
339 test, n= 10, T+ = 50; see SI for additional analysis showing that trial number has no effect).

340

## 341 Discussion

342

343 The chimpanzees developed a successful communicative strategy to coordinate their actions  
344 in a collaborative task. Individuals in the communicator role approached and gave the key to the  
345 recipient close to the box containing the tools, and the recipients correctly inferred from this behavior  
346 the location of the tools that they both needed. The same chimpanzees also made use of the  
347 informative cues of a human experimenter who pointed to the location of the tools from a distance.

348 These results support previous findings concluding that chimpanzees comprehend human  
349 pointing (28). The findings are particularly interesting because these subjects were not language-  
350 trained chimpanzees (as in 25,34), they had never previously participated in a communicative task of  
351 this type, and we employed a more challenging distal pointing as opposed to the proximal pointing of  
352 other previous studies (25,26). One might argue that these sanctuary-living chimpanzees had  
353 experienced a richer socio-communicative environment that had allowed them to learn the meaning of  
354 human informative pointing (34,36). However, it has been previously argued that much more intense  
355 enculturation, than the one typical of sanctuary-living chimpanzees, is necessary to promote apes’  
356 pointing comprehension (26). In our opinion, one cannot rule out the positive impact that daily  
357 positive interactions with humans have on these chimpanzees. However, something else about the  
358 way our study was conducted must have had a positive impact since chimpanzees with similar life  
359 histories did not perform above chance levels in other studies (33).

360 Our study methods differed from previous ones in several ways. First, the subjects  
361 participated in a metacognition pre-test. It is possible that the experience from this pre-test helped the  
362 subjects become more receptive and attentive to the human pointing, perhaps because they understood  
363 that they lacked information to succeed in the task, or because they learned to inhibit the prepotent  
364 response of opening the box straight away. Second, we used a distal set-up in which subjects had to  
365 approach one of the boxes to select it. Mulcahy and Call (27) found that great apes were better at  
366 using human pointing in a distal object-choice set-up and argued that a proximal set-up prevents  
367 subjects from paying attention to the experimenter’s signals (although see 32,33). Third, we used  
368 highly conspicuous signals by combining simulated chimpanzee food-grunts with a pointing gesture  
369 and gaze. Other previous studies (24, 25,38) also found that vocalizations and noises in combination  
370 with behavioural cues facilitated subjects’ performance (although see 32). Therefore, it is possible  
371 that these three factors contributed helping subjects to pay attention to the human. If this is indeed the  
372 case, this would suggest that chimpanzees’ difficulty following social cues is related to inhibitory and  
373 attentional constraints, rather than an inherent inability to understand communicative intentions.



374 Further studies will be necessary to identify the exact factors that facilitate and constraint  
375 chimpanzees' understanding of human social cues.

376 In the critical test of this study, pairs of chimpanzees were required to communicate and  
377 coordinate with each other. We found that the subjects learnt to communicate over the course of the  
378 first experiment with conspecifics. Their communicative behavior consisted of approaching, looking,  
379 touching the box and/or giving the key to the recipient close to the baited box, and these behaviors  
380 increased in frequency during the first twelve trials. The control condition rules out that  
381 communicators were merely attracted to the tools. There are at least two potential explanations for the  
382 emergence of this successful communicative strategy. A lean explanation could be that there was  
383 something similar to a rapid ritualization process during the study regarding the communicators'  
384 behavior and intentionality. Initially, the communicators' approaches to the tools box may have been  
385 unintentionally communicative. The communicators may have approached the box anticipating that  
386 the recipients would open it. The recipients may have occasionally opened it, fulfilling the  
387 communicators' expectations. Soon, the communicators may have intentionally performed this  
388 approach behavior over and over to elicit the recipients' opening of the box. Alternatively, a richer,  
389 but in our opinion more plausible, interpretation may be that the communicators' behaviour was  
390 intentional from the beginning, but only once they made a couple of positive experiences with a  
391 responsive partner they started to communicate consistently. Note that in our previous study with a  
392 different group of chimpanzees (23), chimpanzees also communicated in a similar task, but recipients  
393 ignored them so that communicators stopped communicating. Chimpanzees and other great apes  
394 spontaneously indicate to a human partner the location of food and food-extracting tools (34, 51-52;  
395 see 53 for a review), but whereas chimpanzees have many opportunities to learn the positive effects of  
396 requesting things from humans, requesting things from conspecifics is generally less successful (54-  
397 55).

398 Once communicators were signalling the baited box reliably, the recipients succeeded  
399 obtaining the tools. It might be argued that the recipients simply opened the box to which they were  
400 closest when they obtained the key or that they learnt to associate the cued box with the tools.  
401 Although we cannot completely rule out this explanation, the control condition provides some  
402 evidence to the contrary, since the subjects did not preferentially open the cued box (in the absence of  
403 the communicator), nor were there any signs of improvement throughout the experiment. In  
404 approaching and remaining at one of the boxes, the communicators' behaviour probably resembled  
405 their naturally occurring behaviours when they encounter something interesting (e.g. in a foraging  
406 context). Itakura et al. (24) specifically tested this type of cue in an object-choice task and found that  
407 chimpanzees successfully selected the container approached or examined by a conspecific (or  
408 human). In the current study, the same subjects also performed above chance in the human distal-  
409 pointing comprehension task. Therefore, the most likely explanation is that the recipients also  
410 interpreted the conspecifics' behavior as intentionally communicative.

411 There are several possible reasons for the higher performance of our recipients in comparison  
412 with Bullinger et al. (23) and Moore et al. (55). First, the recipients had already acquired experience  
413 in searching for and attending to relevant information (in the metacognition and human pointing task).  
414 Second, recipients were forced to wait and pay attention to the communicators since the  
415 communicators were in possession of the key to open the boxes. Third, the communicators in our  
416 study provided very evidence-rich expressive behaviors (approaching the baited location and offering  
417 the key necessary to open it nearby), what probably facilitated their understanding of the  
418 communicators' goals (53).

419 In summary, this is the first study to show pairs of chimpanzees developing naturally, without  
420 artificial communicative means (as in 21,22), a successful communicative strategy to ensure  
421 coordination in a collaborative task. Eight out of ten chimpanzees regularly communicated to their  
422 partners the location of the tools. The partners used this information and the result was a successful  
423 form of complex collaboration that included the successful transfer of information between partners  
424 and mutual instrumental support in the form of individuals transferring to each other the necessary  
425 tools. Furthermore, the same subjects were able to use the distal pointing gesture of a human partner  
426 to find the tools.

427 In this study subjects did not need to communicate about a specific tool (as in 21) but just the  
428 tool's location, an arguably simpler task. However, their successful strategy emerged naturally,  
429 without interacting first with a human partner who encouraged them to communicate and fulfilled the

430 recipient's role (as in 21). Subjects in the recipient's role had slightly more experience as they had  
431 participated first in the pointing test with the human partner. However, they only received a small  
432 number of trials with the human partner and the indicative cues used by the human were different  
433 from the ones used by the chimpanzees, so that subjects could not just rely on their previous  
434 experience.

435 These results show that chimpanzees have the capacity to develop new social strategies,  
436 including a communicative strategy, to support each other in their respective roles during a mutually  
437 beneficial collaborative interaction. At the same time these results suggest that for such  
438 communication to emerge and stabilize, subjects need positive experiences with responsive partners.  
439 Future studies could investigate if they are still capable of communicating when they cannot approach  
440 the tool's location, or a simple approach is not indicative enough.

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#### 445 **Acknowledgements**

446 We thank Richard Vigne, the board members and all the staff of Sweetwaters Chimpanzee Sanctuary  
447 in Kenya for their support conducting the research. We also thank Kenya Wildlife Service and NCST  
448 (National Council for Science and Technology, Permit No. NACOSTI/P/15/2619/1321) for allowing  
449 us to collect data in Kenya. This project was generously supported by a grant from the Leakey  
450 Foundation to APM. We thank Wendi Xiang for reliability coding, Raik Pieszek and Martin Millson  
451 for building the apparatuses, Martin Millson for the figures and Roger Mundry for statistical advice  
452 and support. We also thank Federico Rossano and Simon Townsend for comments on an earlier  
453 version of the manuscript.

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## 589 Figure Legends

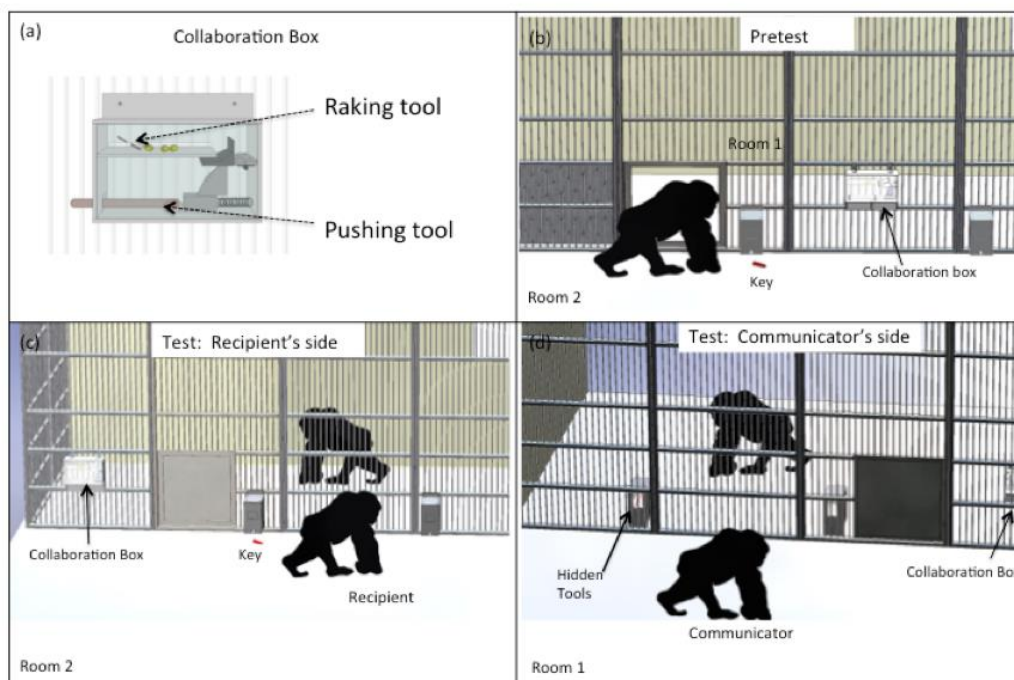
591  
592 Figure 1. Experimental set-up of the study, (a) Collaboration Box from Melis & Tomasello (2013).  
593 One first needs to rake the grapes towards the right side of the box, and then insert the pushing tool to  
594 tilt the platform so that the rakes drop down to both sides of the box. (b) Metacognition individual  
595 Pretest. Individuals entered into room 2 from an adjacent room (room 3). The collaboration box

596 contained grapes inside, and the tools necessary to obtain the grapes were hidden in one of the two  
 597 opaque boxes. Individuals needed to first check the content of the hiding boxes (looking through the  
 598 back of the hiding boxes) and then open with the key the box with tools. Once they obtained the tools,  
 599 they could go back and forth between rooms 1 & 2 to perform both roles and obtain the grapes, (c)  
 600 and (d): Test condition from the recipient's perspective (c) and communicator's perspective (d). The  
 601 communicator can see the location of the tools, but only the recipient can open the hiding boxes. After  
 602 obtaining the tools, the recipient needed to transfer the raking tool to the communicator so that they  
 603 could collaborate emptying the grapes in the collaboration box.

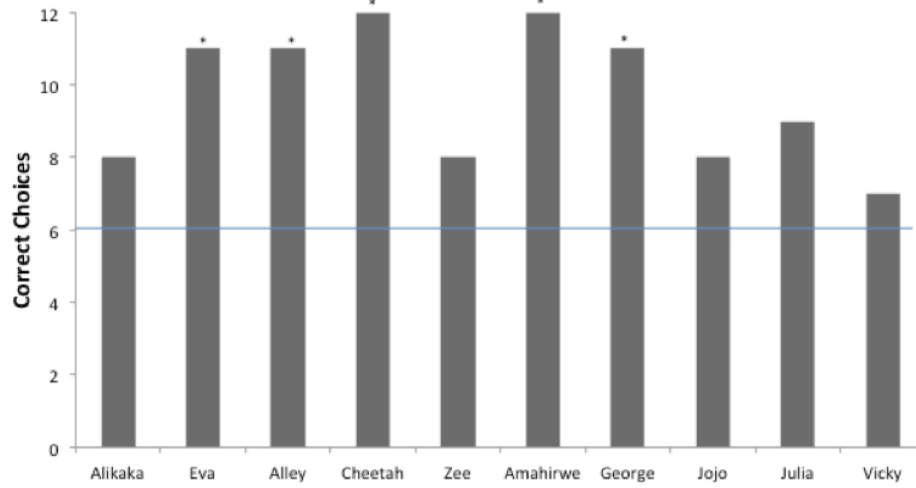
604 Figure 2. Number of correct responses (max. 12 trials) per subject when the human experimenter  
 605 pointed to the location of the tools (\*  $p < 0.05$ , two-tailed binomial probability).

606 Figure 3. (a) Mean proportion of trials (+/-SEM) in the test (i.e. recipients present) and control (i.e.  
 607 recipients absent) conditions of Experiment 2 in which the communicators (N=10) signalled the  
 608 position of the tools. (b) Probability of communication in Experiment 2 as a function of trial number  
 609 and condition (Test vs. Control).

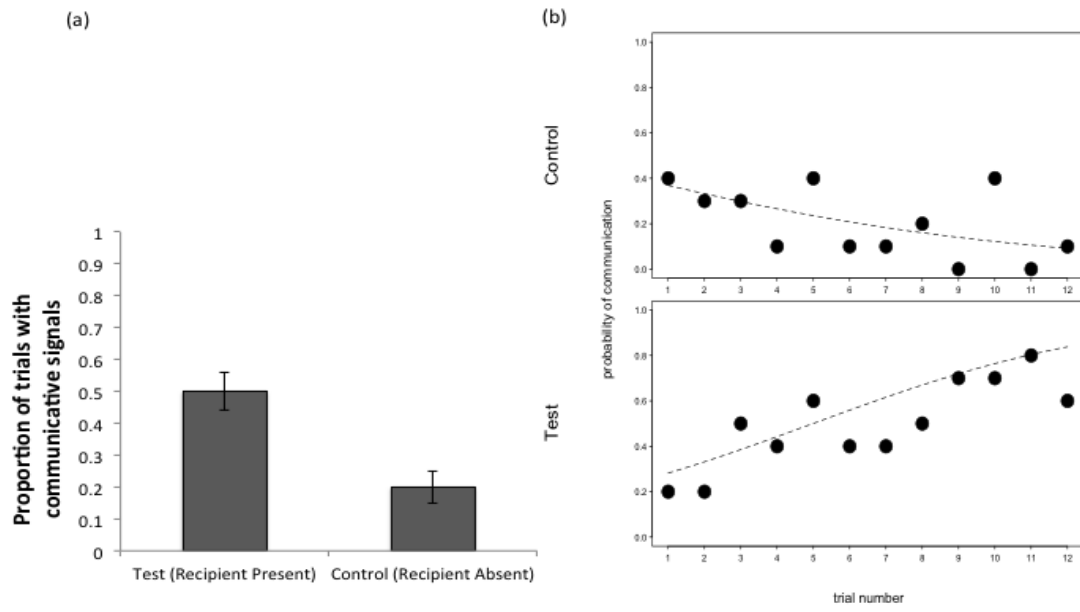
610 Figure 4. (a) Absolute number of trials in Experiment 3 in which subjects in the communicator's role  
 611 signalled one of the boxes (empty or with tools). On the X-axis the subjects in the communicator's  
 612 role with their recipient partners in parenthesis (in the order in which they participated in the  
 613 communicator's role). (b) Absolute number of trials in Experiment 3 in which recipients followed vs.  
 614 did not follow, the communicators' signals. On the X-axis the subjects in the recipient's role with  
 615 their communicator partners in parenthesis (in the order in which they participated in the recipient's  
 616 role).



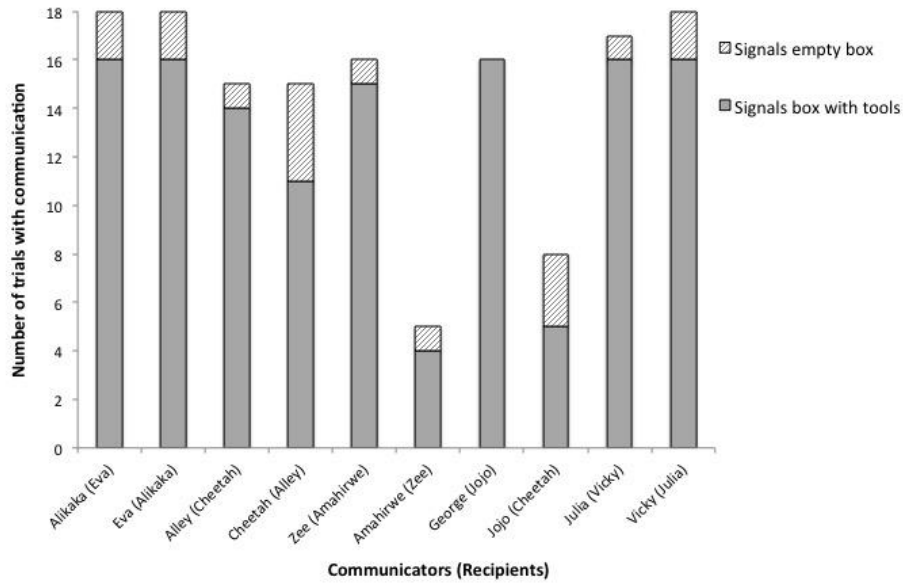
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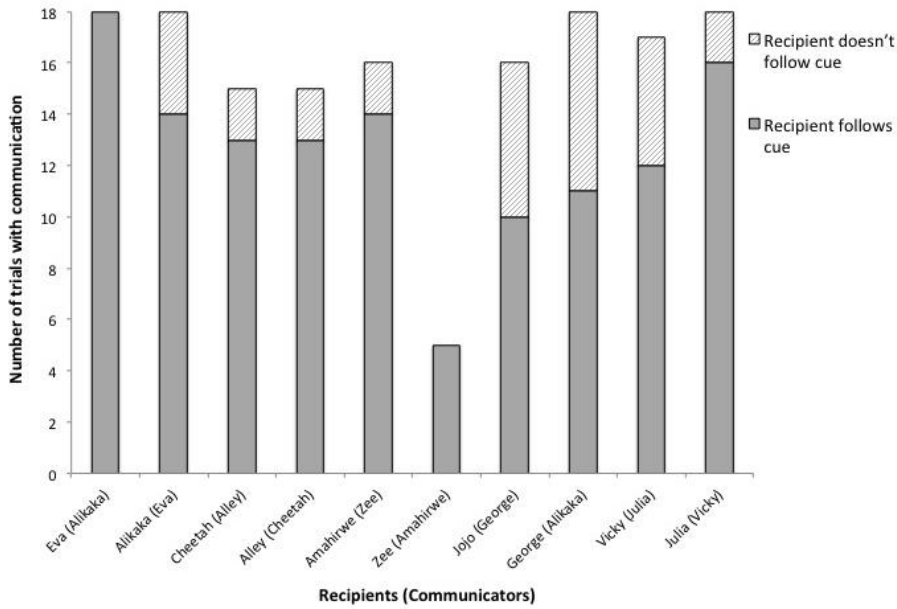
620  
621 Figure 2  
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Figure 4